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Shine and Hide: Biological Photonic Crystals on the Wings of Weevils

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ABSTRACT

The body and elytra of the diamond weevil, *Entimus imperialis*, is studded with numerous brightly colored scales. The scales exhibit brilliant reflections because they contain unusually large diamond-type photonic crystals. The scales are concentrated in pits on the otherwise black elytra. This framing enhances the color contrast when the weevil is observed from nearby. From a distance the diamond weevil looks green, alike green foliage. Another weevil, *Eupholus cuvieri*, has also scales with green reflective photonic crystals, but here the scales are arranged closely apposed on the planar elytra. Both weevils use photonic crystals for camouflage, but the display methods are different.

INTRODUCTION

The brilliant, iridescent body colors of many beetles, butterflies, fish and birds are due to (coherent) scattering of light by nanostructured materials present in the integument [1, 2]. When the refractive index of the biological structures is periodically modulated on the length scale of visible light (i.e. of the order of ~200 nm) with spatial variations in one, two or three dimensions, the structures are acting as photonic crystals. Of extreme interest are the three-dimensional photonic crystals found in insects that are often shaped into one of the three simplest, triply-periodic, bicontinuous-cubic minimal surfaces: primitive cubic (P), diamond (D) or gyroid (G) [3]. Given the low refractive index palette of the biological materials employed in the photonic structures, the reflectance of the biological photonic crystals has become nearly optimal during the long process of evolution [4-6].

In the insect order Coleoptera (beetles and weevils), a diversity of photonic structures has been found [6-8]. Many beetles have multilayers in the elytra (wings) and body, making them highly reflective. In scarabs, helicoidal layered elytra cause bright circular polarized reflections [9]. Even more sophisticated structures exist in weevils, which have three-dimensional, diamond-type photonic crystals. Compared to other structures, diamond-type photonic crystals have the largest photonic bandgaps and the weevils' photonic crystals therefore form a promising candidate for bio-inspired applications [10, 11]. A most intriguing animal is the Neotropical diamond weevil, *Entimus imperialis*. The elytra, body and even legs are studded by brilliantly reflective scales [6, 12]. By electron microscopy, we found that the scales consist of large domains of diamond-type photonic crystals. The domains are randomly oriented, resulting in multi-colored reflections, a unique characteristic of *Entimus imperialis* [12].

Here we compare *Entimus imperialis* with *Eupholus cuvieri*, a weevil with an ordinary scale arrangement, i.e. with photonic crystal domains that are ~10 times smaller. The differences in nanostructures inside their scales as well as in the domain size cause strikingly different appearances of the weevils, which has crucial implications for biological signaling.

EXPERIMENT

The diamond weevil, *Entimus imperialis,* has jet-black elytra with rows of brilliant green spots (Fig. 1A). The spots are actually an assembly of scales, arranged in pits in the elytra. The scales have an elongated shape, with length 100 µm and width 50 µm, and have variously colored domains, ranging in color from turquoise to yellow-orange (Fig. 1C). Most scales consist of a few (three to five) large colored domains (Fig. 1E); a minority of scales, however, has only a single domain and thus has a uniform color [12].

In comparison to *E. imperialis*, the weevil *Eupholus cuvieri* is cyan-green colored, except for a few black stripes (Fig. 1B). The elytron is almost entirely covered with nearly circular-shaped green scales. The scales are closely apposed to the surface and have a diameter of approximately 140 µm (Fig. 1D). The scales are also covered with colored domains ranging from turquoise to yellow-orange; however, the domains are much smaller than those of *E. imperialis* (Fig. 1F).

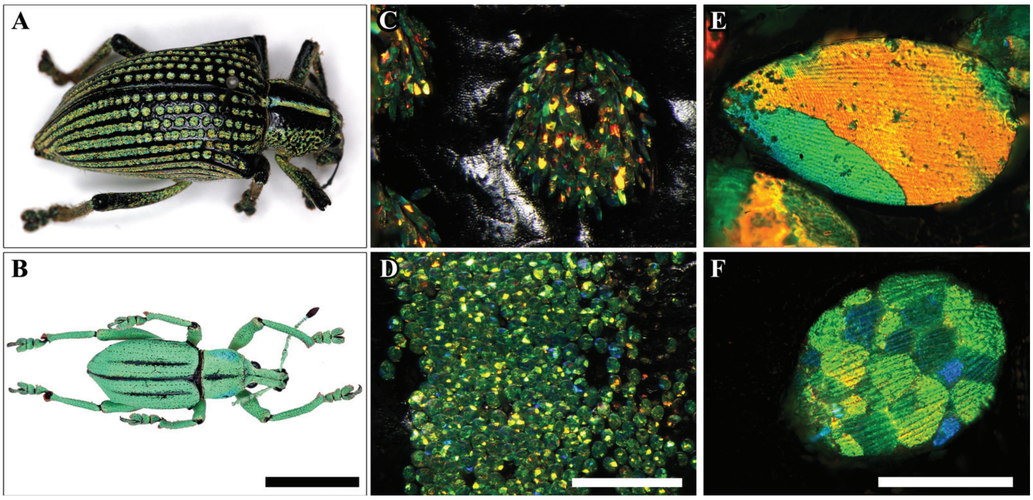

Figure 1. The weevils and their scale arrangement on the elytra. **A** *Entimus imperialis* (subfamily Entiminae of family Curcilionidae). **B** *Eupholus cuvieri* (family Curculionidae). **C** Scale arrangement on the elytra in *E. imperialis*: the scales are arranged in concave pits. **D** In *E. cuvieri* the scales are attached to the approximately planar elytra. **E** A single scale of *E. imperialis*, showing that it consists of only a few colored domains. **F** A single scale of *E. cuvieri* with multiple domains. Bars: (A,B) 1 cm, (C,D) 200 µm, (E,F) 50 µm.

We used scanning electron microscopy (SEM) to investigate the photonic nanostructures inside the scales in detail (Fig. 2). Figure 2A shows the cross-section of a scale of *E. imperialis* where two differently oriented photonic crystals can be distinguished. In an earlier study [12], we have shown that the structures inside the elytral scales are diamond-type photonic crystals that are oriented in specific directions. Each of the photonic crystal orientations can be ascribed to a colored domain of the scale. Figure 2B shows a scale of *E. cuvieri*, where the enveloping cortex has been removed. Here we can discriminate smaller crystal domains, in agreement with the smaller domains of figure 1F. The photonic crystals in both weevils have approximately identical lattice constants, i.e. ~ 440 nm.

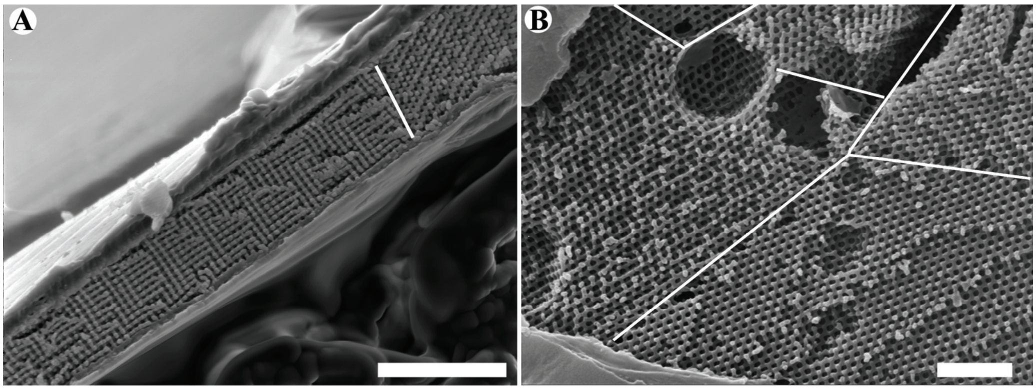

Figure 2. Scanning electron microscopy (SEM) of the photonic crystal structures in weevil scales. **A** SEM image of *E. imperialis*, showing two domains of diamond-type photonic crystals with lattices perpendicular (left of white line) and oblique to the scale surface (right). **B** SEM image of *E. cuvieri*, showing the different local orientations of a number of diamond-type photonic crystals. The hole visible in **B** is the residue of a dead cell's nucleus. The white lines indicate the boundaries between the differently oriented domains. Bars: (A) 5 µm, (B) 2 µm.

To investigate the reflection properties of the different weevil scales, we used a bifurcated probe, which sends light from a light source through six fibers to a small sample surface of ~1 mm^2 - an area equal to that of one elytral pit of *E. imperialis*. The light reflected from the sample was collected with a core fiber. The measured reflectance spectra differed strongly for the two weevils (Fig. 3). Measurements of several pits of *E. imperialis* resulted in various reflectance spectra, two of which are shown in Fig. 3A. The reflectance spectra were all multipeaked, with peak wavelengths between 500 nm and 650 nm. The reflectance spectra measured from the elytra of *E. cuvieri* were, unlike those of *E. imperialis*, uniform, with peak wavelength ~520 nm and half-width ~130 nm (Fig. 3A).

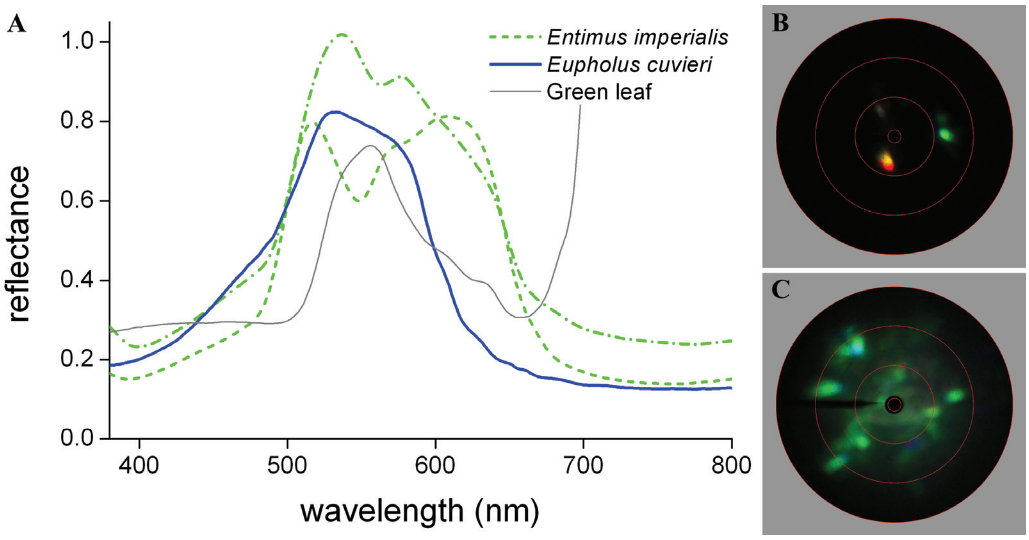

Figure 3. A Reflectance spectra measured with a bifurcated probe of the elytra of *E. imperialis* and *E. cuvieri*, and of a green oak leaf. **B** Scattering diagram of a single scale of *E. imperialis*. **C** Scattering diagram of a single scale of *E. cuvieri*. (Red circles: angles of 5º, 30º, 60º, and 90º.)

We conjectured that we did not obtain a variety of reflectance spectra for *E. cuvieri*, as in *E. imperialis*, due to color mixing because the domains in *E. cuvieri* are very small. To test this assumption, we measured the spatial scattering pattern of single elytral scales with an imaging scatterometer [6, 13]. Illumination of a single scale of *E. imperialis* with a narrow-aperture white-light beam yielded a scatterogram with two distinct, differently colored spots (Fig. 3B), meaning that reflections occurred into two distinct spatial directions. A single scale of *E. cuvieri* created a multitude of mostly greenish spots in the scatterogram (Fig. 3C), meaning that reflections occurred into numerous directions. Nevertheless, overall the reflectance in both cases peaks in the green wavelength range, not too different from the spectrum of a green leaf. This suggests that the scale coloration plays a role in camouflage.

DISCUSSION

Modeling reflectance spectra of single domains

The elytral scales of *E. imperialis* range in color from turquoise to yellow-orange, but the animal's overall color is green. The different colors obviously result from the wavelength-dependent reflection of incident light by the scale structures. This can be quantitatively understood by calculating the reflectance spectra for differently-oriented photonic crystals, applying three-dimensional finite-difference time-domain (FDTD) modeling [12]. The thin gray lines of Fig. 4 represent the averages of reflectance spectra calculated for TE- and TM-polarized light with FDTD modeling for a diamond-type photonic crystal. The thick green line in Figure 4 is the average of the different spectra, which thus represents the case of color mixing. The resulting spectrum well resembles the average reflectance spectrum of *E. imperialis* as well as the spectrum measured from *E. cuvieri* (see Fig. 3A and Ref. 12). Although single scales of *E. imperialis* observed at close range can have various colors (Fig. 1C), when viewed from afar the pits all have a similar green color (Fig. 1A), due to additive color mixing of the different scales.

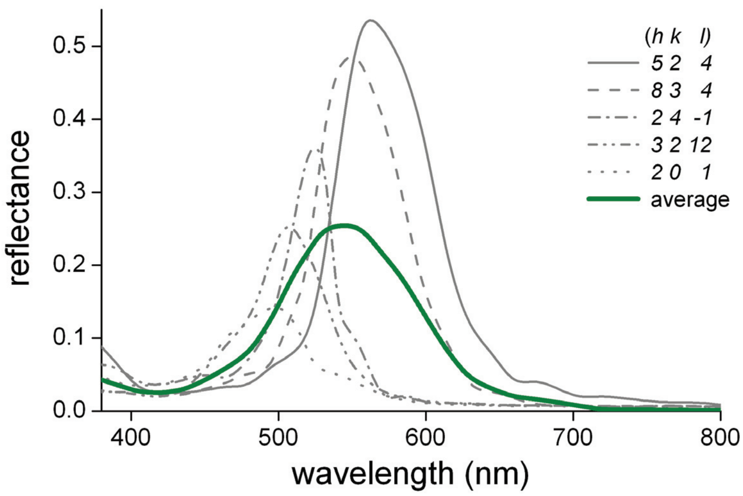

Figure 4. Reflectance spectra calculated with FDTD modeling for a diamond-type photonic crystal when exposed to unpolarized light. Each spectrum represents a different orientation of the photonic crystal, given by the Miller indices, with respect to the illuminating distant point source. The spectra were first calculated for TE- and for TM-polarized light and then averaged.

Spatial visibility and biological implications of the scale arrangement

From the outcome of the bifurcated probe measurements we concluded that *E. imperialis* has a different near-field visibility than *E. cuvieri*, due to the size of the domains on the scales. When the animal is observed at close range, the different domains are large enough to be seen separately, but together they determine the reflectance spectrum measured with the probe. For other weevils, with smaller domains, a rather uniform green color is seen, because the domains can no longer be distinguished, even at close range.

Single scale domains display strong reflections in narrow spatial angles. Given that the spatial angle between adjacent visual axes of the weevils' eyes is in the order of 1 degree, conspecifics will be able to discriminate the reflections from individual domains when the domains are large and seen at close range. This will be the case for the large domains in the scales of *E. imperialis*. Therefore potential mates can discriminate each other's glittering pattern, especially as the scales are concentrated in separate pits. In other words, the pattern created by the scales on the elytra of *E. imperialis* may be used as an intraspecific recognition signal. Most likely this is not the case for *E. cuvieri*.

In the far field, however, both *E. imperialis* and *E. cuvieri* have an overall green appearance that results from additive color mixing of scales in the pits and scales on the elytra, respectively. The over-all green color closely mimics the reflectance of green leaves (Fig. 3A). This suggests that the green color, visible from afar, functions for camouflaging the weevils in their natural habitat. In a preliminary survey, we compared *E. imperialis* with other members of the family Curculionidae that have diamond-type photonic crystals and concluded that *E. imperialis* has an exceptional scale arrangement. The scale arrangement of other family members is comparable with the arrangement of *E. cuvieri*.

Crystal structure

The weevils' photonic crystals were found to have an fcc-symmetry. Using a hemispherical, imaging scatterometer, we were able to directly visualize the Brillouin zones of the photonic crystals [6]. The structural, minimal-symmetry representations were directly discernible in the hemispherical image. Furthermore we were able to measure the directional reflectance spectra of the differently oriented crystals, which allowed the precise characterization of the photonic bandgap diagram of the crystals and thus the determination of the crystal orientation in the scales. The unique possibility of direct imaging of the Brillouin zones provides key insights not only for artificial mimicking photonic crystal structures, but also for non-invasive determination of unknown photonic structures encountered in other animals [6]. The optical properties of the photonic crystals of weevils and other beetles [8, 11] will stimulate biomimetic approaches [2], especially since the routine production of visibly active photonic crystals is still a considerable challenge.

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